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A.P. Kuznetsov, and A.A. Shileyko

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Gutless Protobranchia (Bivalvia)

by A.P. Kuznetsov and A.A. Shileyko

The internal structure of four species of the Solemyida order is described. Petrasma atacama sp. nov. and Acharax eremita sp. nov. have no digestive tract and their labial palps are rudimentary. Nucinella viridula sp. nov. has a weakly developed stomach, but the oesophagus and posterior intestine are absent and the labial palps are very small. N. maxima (Thiele et Jaeckel) has neither a digestive tract, nor labial palps. The reduction of the digestive tube in Solemyida is an independent phenomenon which is not associated with the changes occurring in other organs and systems. The change in the degree of development of the digestive tract in Nucinellina is expressed by significant lengthening of the hindgut. We believe that these changes are of a genetic nature.

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At the end of the 19th century, we already knew that some Protobranchia, namely Solemya togata (syn. S. solen, S. mediterranea) of the Solemyidae family, were characterized by very weak development of the digestive tract combined with hypertrophied ctenidia [13]. The same data were later obtained for other species of this family, and in 1980 Bernard [5] described Solemya reidi, a species with no intestine at all. According to the system of O.A. Skarlatov and Ya.I. Starobogatov [2], the Solemyida order includes two suborders, Solemyina and Nucinellina; only one species belonging to the latter, Nucinella serrei, has been studied anatomically [4]. It has been shown that this

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species with highly developed ctenidia of a "solemyidian" appearance has a normally developed digestive tract, but with a very short posterior part.

The material accumulated over the years by expeditions of the Institute of Oceanology of the USSR Academy of Sciences has made it possible to broaden our knowledge of the Solemyida anatomy. This material is presented and discussed in this paper.

Description of the shells and internal structure of Solemyida species

Superorder Protobranchia

Order Solemyida

Suborder Solemyina

Family Solemyidae

Petrasma atacama Kusnetsov et Schileyko, sp nov. (Fig. 1, A, B).

Locus typicus. "Dmitri Mendeleyev", 20th trip, station 1630, 2 March 1978, depth 105 m, 7°41' S, 79°47' W, Peruvian-Chilean (Atacama) Trench.

Material. 9 specimens.

(40)

The shell is thin-walled, weakly calcified, with a highly developed periostracum which protrudes substantially beyond the edge of the calcareous part. Both an anterior gape, and a posterior gape are present; the periostracal borders are whole, their edges coming together only in the ventral part. The dorsal and ventral margins of the shell are almost straight, and are parallel. A small thickening which encloses a triangular resilium is found right behind the umbones. The posterior end is rounded, the anterior end is almost straight (slightly arched).

There are hardly any radial costae, but radial rays slightly darker than the background are present. There are 8-9 of these rays in the anterior part, and 4-6 in the posterior part of the shell; between these groups of rays, there is another one which is much narrower. The ligament is amphidetic, its anterior part is long, the posterior part is short, triangular, and is supported by one weakly defined costa which circumscribes the edge of the posterior adductor scar anteriorly; the second costa (on the dorsal edge of the scar) is so weakly defined that it is almost indiscernible. The shell is of a dark chestnut colour, but gradually turns lighter near the umbones. Dimensions of holotype (largest specimen): length of shell 14.0 mm, height 5.7 mm, thickness 3.0 mm.

The species is similar to P. valvulus (Carpenter, 1864) (California). It is distinguished from it by the absence of radial striae at the posterior end, and by the presence of a supporting costa of the resilifer.

Internal structure (Fig. 2). Material: holotype and three paratypes.

The foot has numerous, fairly thin papillae along the margin of the sole; contracted, it occupies about one-half of the length of the mantle cavity. The ctenidia are hastate; their posterior ends do not quite reach the posterior end of the mantle cavity. The labial palps are very small, but they are clearly defined and have the form of leaf-shaped appendages located at the posteroventral surface of the base of the visceral sac; the labial palps of different specimens vary in the degree of longitudinal plication. The base of the visceral sac is supported

from below by a well-developed connective-tissue, muscular pulvillus which is a derivative of the tissues of the upper surface of the foot. From the right and left, this pulvillus overlaps the lateral surfaces of the foot; as a result, grooves appear which lead to an area enclosed by the anterior adductor from the front, the base of the anterior part of the visceral sac from the top, and by the dorsal surface of the foot from below. The mouth is usually located in this region, but it is not present in this species, though a small depression is found at the base of the visceral mass. We were unable to detect any traces of a digestive tract with the naked eye. The visceral mass, which also extends into the foot, is composed of elongated acini which apparently represent the sexual gland. After all the tissues of the gonad are removed, we observe the system of anterior pedal retractors. The backmost position is occupied by a single thick strand which medially splits into two closely adjacent branches; in front of this strand at the splitting level, there is a pair of cerebropleural ganglia. The cerebral ganglia are connected by a very short commissure, and are separated from the pleural ganglia by a perceptible vertical groove. The pedal ganglia are relatively small, and the cerebropedal connectives are short. The pleurovisceral connectives extending from the cerebropleural ganglia encompass the sturdy pedal retractor from the sides. Slightly in front of the base of this retractor, there extends a pair of thinner muscular strands which, judging by their position, perform the function of protractors; the nerve branches extending anteriorly from the cerebral ganglia pass between these

protractors. If the pair of retractors is almost perpendicular to the long axis of the animal, the protractors have a more oblique orientation. Finally, several pairs of extremely thin, thread-like pedal levators extend almost perpendicularly from the place of attachment of the protractors to the shell. There is one pair of posterior retractors, which are attached slightly to the front of the posterior adductor. The marginal mantle folds are highly developed; the periostracal borders curve into the mantle cavity even in the region of the gapes. The inner pallial fold forms two specialized areas, in front and at the back. The upper part of the anterior gape bears marginal papillae which are very well-developed in this area, then diminish almost to nil ventrally, and then again become discernible in the lowermost part of the gape, though not to the same extent as in the upper part. The posterior siphon is far more specialized. In the upper part above the siphon proper, there is a short, but basally expanded unpaired papilla which occupies a median position. Then comes the siphon proper - a slit in which the upper part is covered by two pairs of elongated papillae fused at the base. On the right and on the left, there is a row of marginal papillae which increase in size from the top to the bottom. The siphon is closed from below.

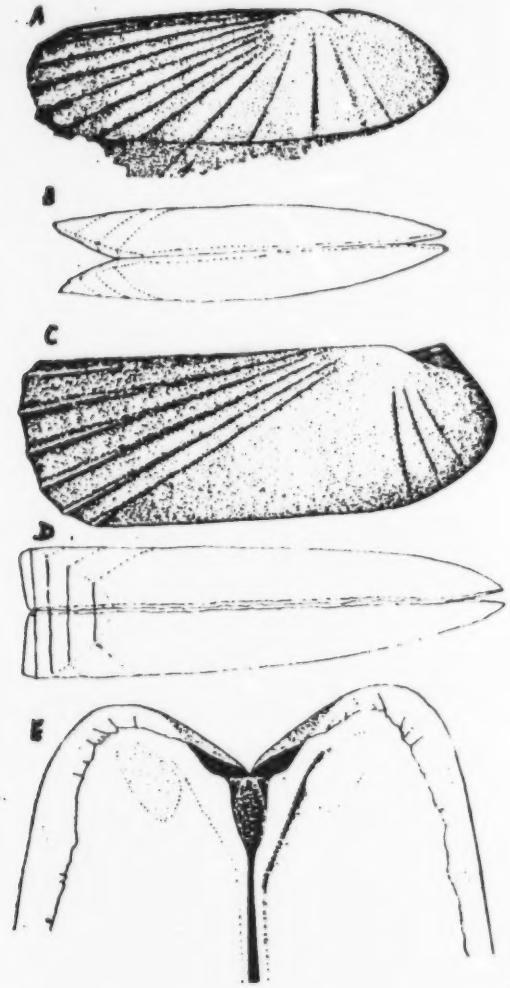

Fig. 1. Shell of Petrasma atacama, sp. nov., holotype (A, B) and Acharax eremita sp. nov., holotype (C-E). A, C - left valves, B, D - ventral view, E - posterior end of shell, view from the inside

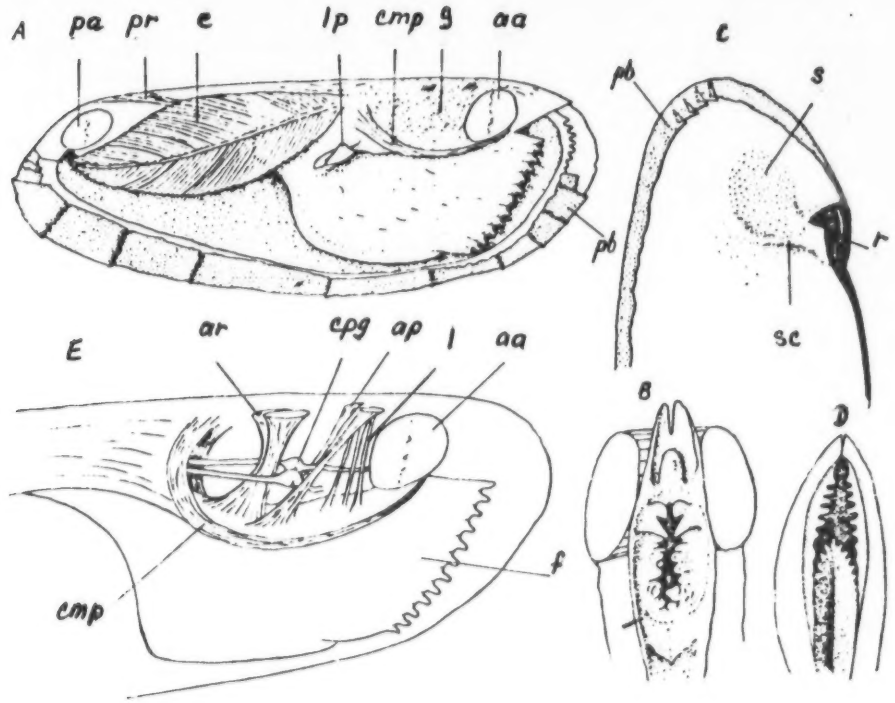

Fig. 2. Structure of Petrasma atacama, sp. nov. A - situs viscera, view from the right; B - posterior siphon, view from behind; C - posterior part of left valve, view from the inside; D - anterior siphon, front view; E - muscle system of anterior end of body, tissues of gonads removed:

g - gonad, pa - posterior adductor, pr - posterior retractor of foot, c - ctenidium, l - levators of foot, lp - labial palps, f - foot, s - scar of posterior adductor, sc - supporting costa of resilifer, aa - anterior adductor, pb - periostracal border, ap - anterior protractors, ar - anterior retractor of foot, r - resilium, cmp - connective-tissue muscular pulvillus supporting visceral sac, cpg - cerebropleural ganglia

Family Acharacidae

Acharax eremita Kusnetsov et Schileyko, sp. nov (Fig. 1, C, D).

Locus typicus. "Vityaz", 31st trip, station 4728, 16 April 1960, depth 900 m, 11°39' N, 49°54' E, Gulf of Aden.

Material. One specimen.

The shell is moderately thin-walled, with a highly developed periostracum which greatly overlaps the edge of the calcareous portion. Only a posterior gape is present; in the anterior part, the periostracal borders of the left and right valves come together at the edges and with moderate contraction of the adductors together form an almost smooth area with a plane perpendicular to the sagittal plane of the animal. The border is whole, and does not form any fringe or digitate expansions anywhere. The dorsal and ventral margins of the shell are parallel, the anterior margin is slightly broadly crimped and almost perpendicular, and the posterior margin is slightly drawn out and slightly angular in the middle. The anterior part of the shell bears six indistinct radial costae on the surface; the most pronounced of these is the first one from the dorsum, and the weakest costa is the sixth one. There are three extremely weak costae in the posterior part of the shell. The shell is of a deep chestnut colour, but becomes slightly lighter toward the umbones; the costae and adjacent parts are darker than the background, almost black, in fact the three posterior costae are detected mainly because of the black colour. The ligament is amphidetic and external; its posterior part is attached to triangular nymphae which stand out because of their black colour. The anterior part of the ligament

extends along the greater part of the dorsal margin, and is clearly seen from the inside when the shell is open. When examining a closed shell from the dorsal or ventral side, we can see that the diameter of the anterior part is greater than that of the posterior part. Dimensions: length of shell 34 mm, height 12.3 mm, diameter 9.3 mm.

It is distinguished from the closest species, A. johnsoni Dall, 1891, mainly by the fact that the periostracal layer is continuous, instead of being divided into separate rays. The ligament is distinctly triangular instead of flattened as in A. johnsoni.

So far, we know of only one specimen of the suborder Solemyina, Solemya cf. occidentalis Deshayes [1], found at depths of 50-261 m in the strait of Bab el Mandeb in the Red Sea. (43)

Internal structure (Fig. 3). Material. One specimen (holotype).

The papillae on the margin of the sole are relatively massive, but not as numerous as in the preceding species. Contracted, the foot occupies slightly less than one-half of the length of the mantle cavity. The labial palps are very small and indiscernible; they have the form of extremely thin leaflets, and are located in the lower part of the visceral mass near the anterior surface of the base of the foot. The connective-tissue muscular pulvillus, which forms the base of the visceral sac, is poorly defined, and the lateral surface of the foot passes almost imperceptibly into the lateral walls of the visceral sac. Weakly defined grooves can be traced from the base of the rudiments of the labial palps; these grooves extend under the base of the

visceral sac and end near a shallow depression in which no mouth has been detected. No traces of any digestive system have been found. The complex of anterior muscular derivatives of the foot is of approximately the same structure as in the preceding species. The marginal mantle folds in the ventral part fuse over quite a distance. There is a set of several pairs of small, but clearly (44)
defined papillae in the upper part of the anterior gape. The posterior siphon is of a much more complicated structure. It is located in the depression between the leaves of the mantle, and the parasiphonal papillae are arranged in three clearly defined groups. In the upper part, relatively small papillae are arranged in 2-3 poorly defined vertical rows, the papillae forming the lateral rows being the largest; farther down, there is an area without any papillae at all; only the very edge of the siphonal slit bears a multitude of very small, sessile, tuberculate papillae. Finally, there are three pairs of large papillae below the siphonal slit.

Suborder Nucinellina
Family Nucinellidae

Nucinella maxima (Thiele et Jaeckel, 1931) (Fig. 4, A, B, E, F).

Thiele, Jaeckel, 1931: 188, Plate 1, Fig. 28 (Pleurodon maximus).

Locus typicus. Zanzibar Channel, 5°27'9" S, 39°18'8" E, depth 463 m.

Since this species was first described on the basis of one (right) valve, we have described the only shell available to us. Coordinates: "Vityaz", 31st trip, station 4794, 28 Oct 1960, depth 393 m, 12°02'6" N, 51°11'1" E (Gulf of Aden).

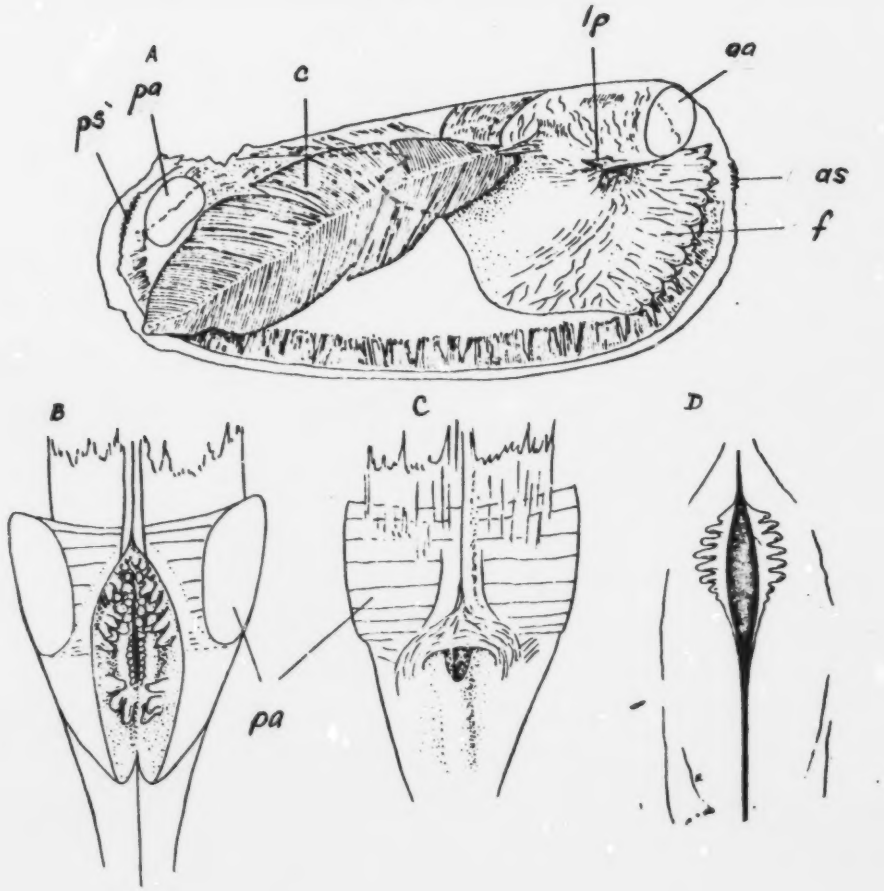

Fig. 3. Structure of Acharax eremita, sp. nov. A - situs viscera, view from the right; B - posterior siphon, view from behind; C - posterior siphon, front view (from the inside); D - anterior siphon, front view:

ps - posterior siphon, as - anterior siphon; remaining nomenclature as in Fig. 2

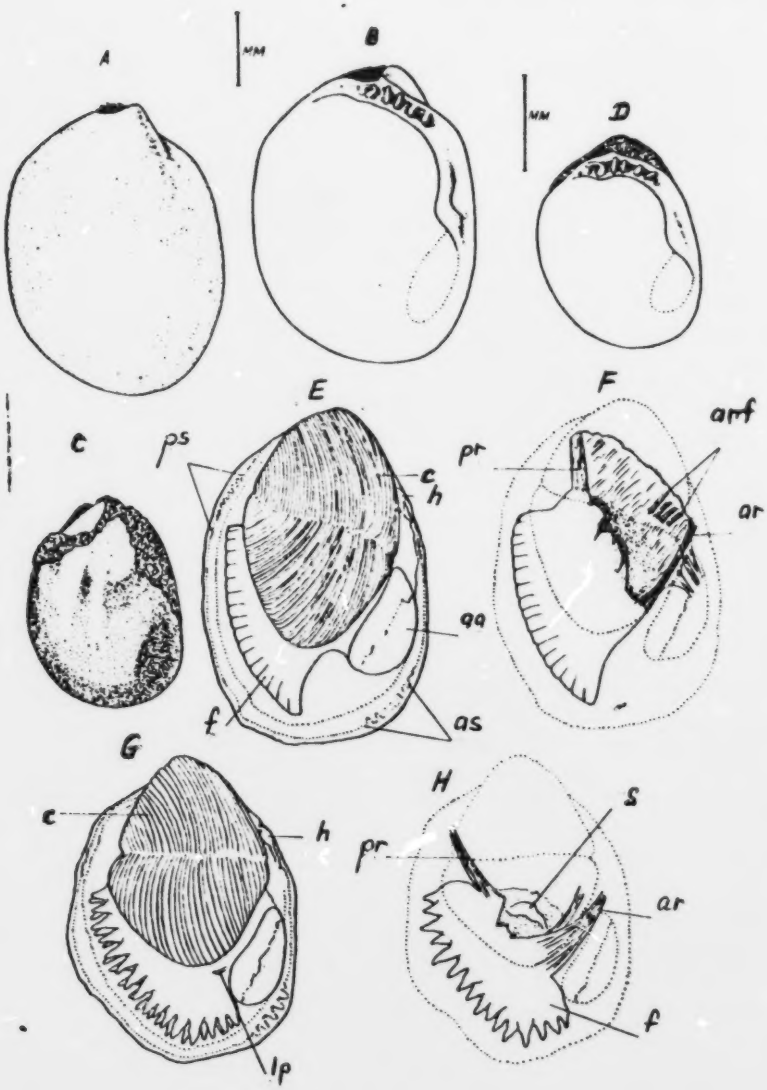

Fig. 4. Shell and internal structure of Nucinella maxima (A, B, E, F) and N. viridula, sp. nov. (C, D, G, H). A, C - right valves; B, D - left valves; E, G - situs viscera, view from the right; F, H - muscular derivatives of foot:

arf- accessory retractors of foot, s - stomach, h - heart; remaining nomenclature as in Figs. 2 and 3

The shell is oval, comparatively thick-walled, shiny, with slightly protruding umbones. The dorsal margin is straight, sloping, passes into an almost straight anterior margin with a slight, but clearly defined angle. An even more flattened angle is found at the point where the anterior margin passes into the ventral margin which together with the posterior and postero-dorsal margins forms a broad and gently sloping arc. The perio-stracum is thin, greyish yellow, with a barely perceptible greenish hue. There is hardly any sculpture. The hinge area is well-developed; in the right valve, there is one thin, lamellar, high, triangular lateral tooth and six cardinal teeth, two of which are found under the ligament. In the left valve, there are two lamellar lateral teeth (external tooth smaller than internal one), between which the tooth of the right valve fits; there are six cardinal teeth, one which is found under the resi-lium and is connected with the adjacent one by means of a pecti-nate septum in the upper part. The shell measures 3.1 mm in length, 4.2 mm in height and 2.5 mm in diameter.

The holotype is distinguished from our specimen by much larger dimensions (height of shell 12.5 mm), but because of insufficient material, we cannot establish whether this difference is due to the young age of our specimen, or the population of the Gulf of Aden is made up of smaller specimens. There are also some dif-ferences in the closing apparatus. In the illustration to the initial description, the three backmost cardinal teeth are not parallel to the others, are lamellar and almost push against the upper edge of the hinge area; the three back teeth on the right valve of our specimen are not quite parallel to the rest, are

only slightly drawn out, are sooner tuberculate than lamellar, and obviously do not extend to the outer margin of the shell.

Nevertheless, since only one specimen was available to us, we do not consider it advisable to describe the new species.

Internal structure. Material. One specimen.

The foot has numerous papillae along the margin of the sole; in a fixed specimen, they are curved under and cannot be seen from the side (only notches are seen along the edge of the sole). The sole is located in the mantle cavity parallel to the posterior margin of the shell, and extends slightly onto the ventral margin. Labial palps are not encountered. The visceral sac is covered with a connective-tissue muscular sheath and is slightly embedded in the foot. The tissues that form the visceral sac are difficult to differentiate macroscopically; they consist of a fairly homogeneous mass of an off-white colour, in which we can distinguish individual acini that apparently represent the sexual gland. The degree of gonadal development is still an open question. Neither a mouth, nor any traces of a digestive tract could be detected. The system of pedal retractors consists of a pair of sturdy adjacent posterior muscular strands and a pair of anterior ones; both pairs extend from the respective backmost and frontmost parts of the base of the foot. In addition, three pairs of thin muscular bundles extend forward from the sheath enveloping the visceral sac on the right and on the left of the adductor, (46) while four thin, upwardly directed retractors extend from the inner surface of the sheath on each side. The ctenidia are very large and occupy the greater part of the mantle cavity; the ctenidial axis forms an acute angle with the dorsoventral axis of

the body. The margin of the mantle slightly below the adductor bears six or seven pairs of minute, but fairly discernible papillae; on the posterior margin opposite the middle of the ctenidia (upper part of the margin), there are several more pairs of smaller papillae which diminish to nil in the upper and lower parts. No traces of mantle fusion have been detected.

Nucinella viridula Kusnetsov et Schileyko, sp. nov.
(Fig. 4, C, D, G, H)

Locus typicus. "Dmitri Mendeleyev", 16th trip, station 1269, depth 710-720 m, 44°27' S, 174°28' E (near New Zealand), one specimen.

The shell is oval, very thin-walled, shiny, with slightly protruding umbones. The shell surface of the only specimen is covered in its upper parts with a ferromanganese crust, and so it is difficult to tell to what extent the umbones protrude. The anterior part of the dorsal margin is short, almost straight, and with a slight curve passes into a very weakly arched anterior margin. The ventral and posterior margins form a gently sloping arch which passes into a straight posterodorsal margin with an insignificant angle. The periostracum is highly developed and greenish in colour. The sculpturing consists of highly eroded, weakly defined concentric folds. The hinge area is relatively very large, and each valve bears one lamellar, triangular lateral tooth. There are five cardinal teeth in each valve; the anterior cardinal tooth in the left valve is oriented almost across the dorsoventral axis of the shell, the third and fourth are parallel to this axis, and the second one occupies an intermediate position. The third and fourth teeth are the highest and thinnest (lamellar).

The fifth and sixth teeth in the upper part are joined by a thin bridge. The shell measures 1.4 mm in length, 2.2 mm in height and 1.5 mm in diameter.

The shell contour is very reminiscent of the shell contour of N. hedleyi described from Australian waters [6], but the latter has longer lamellar cardinal teeth. The greenish colour makes this species similar to N. viridis, recently described from Japan [7], but this species is much larger (9.9-10.4x7.3-7.8 mm).

Internal structure. Material. One specimen (holotype).

The foot bears numerous large conical papillae which do not curve onto the sole. The latter lies parallel to the posterior and ventral margins. The labial palps are rudimentary, minute, in the form of very fine outgrowths on the lateral surfaces of the upper part of the foot slightly behind the lower part of the adductor. The visceral sac is covered with a connective-tissue muscular sheath with a multitude of very weakly differentiated acini inside it; among these acini, there lies a rudimentary stomach which has preserved a gastric shield, but no mouth, oesophagus, nor hindgut could be detected. The stomach is irregularly fusiform, drawn out in an anterior-posterior direction. We must emphasize that it would be premature to say that this species has no intestinal tube, as we had only one very small specimen to work with, and no microscopic examination was carried out. We can say with certainty that the system of pedal retractors consists of only two pairs, an anterior (stronger) pair and a posterior one. The ctenidia are large, though relatively smaller than in the preceding species; their axis is perpendicular

to the dorsoventral axis of the body. In the region of the lower part of the adductor, the margin of the mantle bears five pairs of clearly discernible, relatively large papillae; the posterior exhalant aperture is also fringed with papillae, but here they are very small, poorly discernible and difficult to count, as they gradually diminish to nil. (47)

Discussion of results

The question of how gutless bivalve mollusks feed has been discussed many times, and since we have nothing new to add to the available data, we refer the reader to the papers by Owen and Reid [10, 11]. However, we do believe that this problem should be resolved in general terms, without limiting ourselves to bivalve mollusks, since there are other macroscopic organisms without a digestive tract (Pogonophora, some of the Annelida). At this point, we would like to draw your attention to two other questions, i.e. the functional interpretation of the mantle water currents and the related mechanisms and phenomenon of parallel variability of the digestive tract in Protobranchia.

Water movement in the mantle cavity of various Solemyida

The mantle water currents perform at least four vital functions, i.e nutritional, respiratory, purifying (excretion of pseudofeces) and locomotory (when swimming). The latter stands by itself and is accomplished by means of muscular mechanisms (the foot), while the other three are accomplished by means of ciliary mechanisms.

We know from the literature [8, 10, 11, 15] that the water currents in the mantle cavity move from the front to the back,

and therefore the water enters through the anterior siphon (anterior gape) and is discharged through the posterior one. On the whole, the front to back current probably really does prevail, but we do not think that this phenomenon should be interpreted unequivocally, as the situation is really more complex.

Assuming that only a front to back water current exists in these animals, it is difficult to explain the presence of the complex morphological armature of the posterior (exhalant) siphon. Indeed, the i n c o m i n g current from the front passes through a very simple single-row system of papillae, which can serve as a coarse filter and control the quality of the incoming water. At the same time, a complex and specialized apparatus consisting of several types of papillae of different shapes and sizes is for some reason or other found in the path of the water l e a v i n g the mantle cavity (a simple opening would do in this case).

This situation prompts us to surmise that, at certain times, water enters the mantle cavity through the posterior siphon as well, especially as Reid [11] has shown that a well-defined anteriorly directly water current exists at the point of attachment of the ctenidia to the foot, a current which is generated by the cilia of the base of the foot and by the lateral cilia of the ctenidial lamellae. Furthermore, Morse and Owen [8, 10] have observed that the slit of the posterior siphon is capable of dividing into two independent openings; the outgoing current can leave the mantle cavity through both openings, or only through

one of them; in the second case, the second opening is partially closed.

Various assumptions are possible here, but the most probable one is that the nutritional and purifying functions are carried out with anterior-posterior movement of the water in the mantle cavity, while the respiratory function is carried out with posterior-anterior movement of the water. Assuming that the direction of the water current changes periodically, it becomes clear why there is such a significant difference in the structure of the anterior and posterior siphons; after all, purer water is needed for respiration, and the complex system of papillae in the posterior siphon is certainly a more effective filter than the morphologically simple anterior siphon. Furthermore, the diversity of the papillae of the posterior siphon points to the precise adjustment of the force and direction of the incoming flow of water; this is especially important in connection with the fact that the posterior ends of the ctenidia are located directly behind the posterior siphon. (48)

The temporary division of the posterior siphonal slit into a ventral and a dorsal section prompts us to assume that the excretion of pseudofeces (through the ventral section) and the intake of a respiratory water current (through the dorsal slit) can take place simultaneously. Proof of this is the spatial division of currents of different directions [11], i.e. if a posteriorly directed current is formed mainly by cilia on the ventral surfaces of the ctenidial septa, then the anterior current (as mentioned earlier) passes higher up and more laterally.

So far, we have spoken only of the suborder Solemyina. As for the Nucinellina, no information is available on the mantle water currents in this suborder. However, judging by the simple and very similar structure of the anterior and posterior openings, as well as by the absence of mantle fusion in the ventral part, the water flows in one direction in their mantle cavity.

Parallel variability in the structure of the digestive tract of Protobranchia

At first, let us recall what we know about the degree of development of the intestinal tube in the order Solemyida. The list given below includes only the living families and genera; the letters "N", "R" or "A" in brackets after the names of the species signify that the digestive tract is either normally developed (N), rudimentary (R), or absent altogether (A). The data are from the literature [5, 8, 9-13, 15]. The spacing of the names of some species means that these species are being examined for the first time.

Suborder Solemyina

Solemyidae

Solemya: *togata* (R), *parkinsoni* (R), *reidi* (A)

Petrasma: *valvulus* (R), *velum* (R), *panamensis* (R), *borealis* (A), *a t a c a m a* (A)

Acharacidae

Acharax: *agassizii* (R), *johnsoni* (R), *e r e m i t a* (A)

Suborder Nucinellina

Huxleyoidae: not a single species studied

Nucinellidae

Nucinella: *serrei* (N), *v i r i d u l a* (R), *m a x i m a* (A)

Thus, if complete reduction of the intestine was previously regarded as a phenomenon unique to the bivalve mollusks and observed only in the genus Solemya from the family Solemyidae, the data in this paper show that this phenomenon is quite common in the order Solemyida. Consequently, one can speak of the independent and parallel reduction of the digestive tract, which manifests itself at least three times in both suborders, i.e. among the Solemyidae, among the Acharacidae (suborder Solemyina) and among the Nucinellidae (suborder Nucinellina). Perhaps the ease with which the digestive tract is lost in the Solemyida has deeper roots, and the "lability" of the digestive apparatus is on the whole characteristic of the superorder Protobranchia.

Whereas the hypertrophied ctenidia in the order Solemyida contributed to the tendency of intestinal reduction, "lability" of the digestive tract is also known in the order Nuculida, though the "lability" here takes on an entirely different form. We are speaking of the family Ledellidae. The genera Bathyspinula and Ledella, besides including species with one loop of the hindgut (B. calcar, L. ultima), contain species with 4-11 loops of the hindgut (the remaining species of the genus Bathyspinula and many species of the genus Ledella) [3]. Naturally, in all of these cases, the pronounced hypertrophy (Nuculida) or reduction (Solemyida) of the digestive tract are an independent phenomenon which in no way reflects on the structure of any of the other organs or systems. (49)

The independence of the "behaviour" of the digestive tract is also seen in the fact that its state cannot be related to any

external conditions, specifically the depth of the habitat. For instance, Ledellidae with one intestinal loop are occasionally encountered alongside forms with numerous intestinal loops; Nucinella serrei is found at depths of 400-500 m (digestive tract normally developed), N. maxima at a depth of about 400 m (digestive tract absent) and N. viridula at a depth of 700 m (digestive tract rudimentary).

Assessing the situation as a whole, one can say that the digestive apparatus in the superorder Protobranchia sometimes acquires, for reasons unknown, an unprecedented "lability" (figuratively speaking), and its reduction (in Solemyida) or hypertrophy of some of its elements (in Ledellidae from the order Nuculida) manifests itself as an independent phenomenon which does not involve the other structural characteristics of the animals. Since the dependence of morphological change on external conditions cannot be traced, one can assume that the variability of the digestive apparatus in this case is of a genetic nature.

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